

STUDIES ON THE INHERITANCE OF RUST RESISTANCE IN OATS

IV. EXPRESSION OF ALLELOMORPHISM AND GENE INTERACTION FOR CROWN RUST RESISTANCE IN CROSSES INVOLVING THE OAT VARIETY BOND

E. P. BAKER and Y. M. UPADHYAYA

Department of Agricultural Botany, The University of Sydney

[Read 28th September, 1966]

Synopsis

Segregation for crown rust reaction type was studied in the F_2 and F_3 generations in both seedling and adult plant stages in crosses between the resistant variety Bond and susceptible varieties and in crosses between Bond and the varieties Landhafer, Santa Fe, Trispermia, Mutica Ukraine (Ukraine) and Victoria, all resistant to the prevalent Australian races. The immunity of Bond was conditioned by two dominant genes, acting in complementary fashion, in both stages of growth. However dominance was incomplete at high temperatures, modifying the characteristic F_2 9 resistant : 7 susceptible ratio to a corresponding 5 : 11 ratio. The studies extended the genes for resistance identified in certain of the resistant varieties. Landhafer was found to have a third factor acting in complementary dominant fashion with one of the two complementary Bond factors in conditioning seedling resistance only. A third factor in Santa Fe was a complementary dominant factor to the same member of one of the two Bond factors. It was effective in conditioning resistance in both seedling and adult plant stages. The fifth factor in Ukraine was a third member of the allelic series at one of the Bond loci. Fulghum and Algerian contributed the fourth member of the allelic series at one of the Bond loci and acted in complementary fashion with the second Bond gene to confer adult plant resistance only. Grass clump type segregates were observed in the F_2 generation of the cross between Bond and Landhafer. The segregation ratio suggested the genetic action of an inhibitor gene to a dominant gene for grass clumping.

INTRODUCTION

The oat variety Bond has proved a valuable source of resistance to crown rust (*Puccinia coronata avenae* Erikss.) in North America in breeding improved varieties. It originated in Australia as a selection from a cross made by Pridham at Cowra Experiment Farm between the variety Golden Rain and an offtype of the Red Algerian variety introduced from Algeria. Resistance to most races of crown rust and some races of oat smuts was incorporated into Bond; resistance to the latter diseases apparently was transferred from the Red Algerian parent. Reference to the mechanisms involved in the incorporation of crown rust resistance will be considered later. In addition, Bond possesses the agronomic virtue of stiff straw.

With the increase in prevalence of crown rust races attacking Victoria derivatives in North America and the susceptibility of these varieties to Helminthosporium blight (*Helminthosporium victoriae* Meehan and Murphy) considerable attention was turned about 1945 to the production of commercial varieties deriving resistance from Bond. Several important economic varieties were subsequently released from Bond crosses. However, with the popularity of such derivatives, race 45 of crown rust, capable of attacking Bond and its derivatives, increased tremendously. As a result the varieties Landhafer, Santa Fe and Trispermia have been used more recently in breeding for rust resistance.

In Australia Bond, included in the international differential varietal crown rust set in physiological race surveys, was resistant until 1949, when Waterhouse (1952) isolated two races capable of attacking it from field collections. Investigations by Baker and Upadhyaya (1955) for the period 1953-55 showed that races virulent on Bond were not prevalent and Bond remained a good source of resistance for the breeding of resistant varieties.

In the results presented in the current paper the mode of inheritance of crown rust resistance in Bond was analysed. The factors present in Bond were also shown to interact, or to be allelic, with factors in other resistant and, in certain instances, susceptible varieties. Genetic independence or otherwise between the Bond genes and the stem rust resistance gene (Rd_1) in Richland was also studied.

LITERATURE REVIEW

Crown rust resistance in Bond has been shown to be conditioned by a pair of dominant complementary factors by several investigators (Hayes *et al.*, 1939; Weetman, 1942; Cochran *et al.*, 1945; Ko *et al.*, 1946; Litzenberger, 1949; Kehr and Hayes, 1950; Griffiths, 1953). However, Torrie (1939) obtained an F_2 ratio approximating 11 susceptible : 5 resistant plants, and interpreted the results on the basis of the action of a strong gene in Bond with another masking its effect. At the same time this ratio was explained by Hayes *et al.* (1939) and Ko *et al.* (1946) on the basis of a very weak expression for resistance when both complementary factors in Bond were present in the heterozygous condition.

Modifications of the above reported ratios were observed by certain workers. Apparent segregation of a single factor due to the common presence of one of the complementary Bond genes was reported in crosses between Bond and the varieties Iogold (Hayes *et al.*, 1939) and Santa Fe (Litzenberger, 1949). Whilst Finkner *et al.* (1955) reported the operation of a single factor in Bond from observations on the cross of its derivative, Clinton, with Ukraine, Osler and Hayes (1953) detected the presence of non-identical allelomorphs in the variety Santa Fe. Weetman (1942) from field data indicated that resistance in Mutica Ukraine to race I was due to two dominant complementary genes. He suggested that the factors in Ukraine were probably allelomorphs to the Bond genes for resistance.

Inhibition of the factors for resistance in Bond has been reported by certain workers. Richland-Fulghum possessed two complementary inhibitors (Cochran *et al.*, 1945), Ukraine possessed one factor for seedling resistance to race 57 and this gene inhibited the resistance of Clinton against race 109 (Finkner *et al.*, 1955); undetermined factors in S.D. 334 (a Richland derivative) inhibited the resistance of Bond resulting in an F_2 ratio of 15 susceptible : 1 resistant plant (Ko *et al.*, 1946).

Studies on the mode of inheritance of crown rust resistance in the varieties Landhafer, Santa Fe, Mutica Ukraine and Victoria have been reviewed in previous papers in this series (Upadhyaya and Baker, 1960; Upadhyaya and Baker, 1962b). Against Australian races Landhafer possessed two factors for adult plant resistance, one of which conditioned seedling or physiological resistance in addition; Santa Fe possessed one factor operative in both seedling and adult plant stages; Mutica Ukraine (henceforth designated as Ukraine) possessed one factor for seedling resistance independent of the three factors for adult plant resistance (two of which acted in complementary fashion). The Victoria type crown rust resistance was conditioned by two linked complementary factors (with a linkage value of 9.6 ± 1.7) in the seedling stage, by two independent factors operative at the adult plant stage only and by one independent factor operative at both stages. The action of the latter factor was inhibited by a linked gene showing approximately 10% recombination with it. One of the factors for adult plant resistance was linked with approximately 10% recombination with the two linked complementary factors for seedling resistance.

Upadhyaya and Baker (1965) studied the relationships of the genes for resistance in the varieties Landhafer, Santa Fe, Trispermia, Ukraine and Victoria to the prevalent Australian races of crown rust. The two factor pairs in Landhafer conditioning adult plant resistance, one of which conferred seedling

resistance in addition, were independent of the factors in the varieties Santa Fe, Trispermia and Victoria. The seedling reaction type of Landhafer was epistatic to those of Trispermia and Victoria. The factor for both seedling as well as adult plant resistance in Santa Fe was independent of the factors in Victoria and epistatic to them. Certain modifying gene(s) resulted in the expression of a reaction type similar to that characteristic of Victoria by suppressing the Santa Fe gene. The Santa Fe factor was considered allelic to the factors in Ukraine and Trispermia. The reaction type of Santa Fe was dominant to that of Trispermia in tests with four races, but with race 203 the Santa Fe gene was inhibited by a pair of complementary factors, one contributed by each variety. The three factor pairs in Ukraine, two acting in complementary fashion, involved in adult plant resistance were independent of the Santa Fe gene. Indirect evidence indicated that the factors conditioning seedling resistance in Santa Fe and Victoria were genetically independent. The independence of the factors responsible for adult plant resistance in Landhafer and Ukraine and likewise the independence of the Ukraine and Victoria adult plant factors could not be established in the absence of studies involving the appropriate crosses.

Upadhyaya and Baker (1962a) showed that the oat varieties Burke and Laggan possessed a single gene (Rd_1) operative against races 2 and 12 of stem rust (*P. graminis avenae* E. and H.).

EXPERIMENTAL RESULTS

The experimental procedure was as set out by Upadhyaya and Baker (1960).

(A) *Studies on Inheritance of Crown Rust Resistance*

Crosses involving Bond with the following varieties were studied :—

Fulghum, Algerian, Burke and Laggan—susceptible to all crown rust races used.

Santa Fe, Landhafer, Ukraine and Victoria—susceptible to only specific races of crown rust.

(a) F_1 Reaction Types and Reactions

The reaction types and reactions of the parents and F_1 's are presented in Table 1.

The adult plant immune reaction and highly resistant reaction seedling type ("0 ; ") characteristic of Bond was dominant or partially dominant in crosses involving specific races where the second parent was susceptible. Likewise where both parents were resistant the immunity or highly resistant reaction type of Bond was usually epistatic or partially so. However, in certain cases a slightly less resistant reaction than either parent was observed in the mature plant stage. Incomplete dominance of the reaction or reaction type of resistant parents was observed in the case of race 203 to which Bond was susceptible.

To field inoculum, comprising a mixture of races, none of which were, however, virulent on Bond the reactions of the F_1 plants in Bond crosses were intermediate or moderately susceptible. In certain cases slightly variable reactions were exhibited among different F_1 plants in the same cross.

(b) *Behaviour of Segregating Generations Involving Races to which only Bond was Resistant*

(1) F_2 Segregation

(i) Seedling tests

Data relating to these tests are presented in Table 2.

In crosses between Bond and Fulghum, Algerian, Burke, Santa Fe and Ukraine a satisfactory agreement between observed and expected results for each F_2 population was observed on the basis of segregation of two dominant complementary factors contributed by Bond. The total segregation of the separate plants in each cross and the grand total for all crosses also agreed

TABLE 1
Parental and F₁ seedling reaction types and adult reactions in crosses involving the oat variety Bond

Parent or cross	Seedling reactions to races							Reactions in the adult stage					Field
	203	226	237	237-4	259	286		203	226	237	237-4	259	
Bond	S ¹	I	I	I	I	I
Fulghum	S	S	S	S	S	S
Algerian	-	-	-	-	-	S (98%)
Burke	-	-	-	-	-	S
Laggan	-	-	-	-	-	MS
Santa Fe	I	I	I	I	I	I
Ukraine	I	I	I	I	I	I
Landhafer	I	I	I	I	I	I, MR-Int.
Victoria	R	R	R	R	R	I (98%)
F ₁ Fulghum × Bond	-	-	-	-	-	Int.-S
F ₁ Algerian × Bond	-	-	-	-	-	Int.-R
F ₁ Burke × Bond	-	-	-	-	-	Int.-S
F ₁ Laggan × Bond	-	-	-	-	-	I, R-MR
F ₁ Santa Fe × Bond	R	R	R	R	R	-
F ₁ Ukraine × Bond	-	-	-	-	-	Int.-R
F ₁ Landhafer × Bond	R	R	R	R	R	Int.-R
F ₁ Victoria × Bond	-	-	-	-	-	Int.-R

¹ I = immune, R = resistant, MR = moderately resistant, Int. = intermediate reaction, S = susceptible.

statistically with the expected 9 resistant : 7 susceptible F_2 seedling ratio. The data for the totals of each cross were also homogeneous. Figures for the crosses Fulghum \times Bond and Burke \times Bond, tested against race 286, where the frequencies were corrected from F_3 behaviour, are not included in the Table.

TABLE 2

F_2 seedling segregation for crown rust reaction type in crosses involving Bond and certain susceptible varieties

Cross	Crown rust race	F_2 reaction types				Total	Expected ratio	P value
		Resistant 0;	1 2-	Susceptible 3-4				
Fulghum \times Bond ..	226	119	41	1	122	283	9 Res. : 7 Sus.	0.90-0.80
	259	60	10	-	58	128	9 Res. : 7 Sus.	0.80-0.70
Total			231		180	411	9 Res. : 7 Sus.	1.00
Algerian \times Bond ..	226	54	8	-	46	108	9 Res. : 7 Sus.	0.90-0.80
	237-4	30	21	-	50	101	9 Res. : 7 Sus.	0.30-0.20
	286	63	45	2	97	207	9 Res. : 7 Sus.	0.50-0.30
Total			223		193	416	9 Res. : 7 Sus.	0.30-0.20
Burke \times Bond ..	259	89	50	2	125	266	9 Res. : 7 Sus.	0.30-0.20
Santa Fe \times Bond ..	286	238	80	43	274	635	9 Res. : 7 Sus.	0.90-0.80
Bond \times Ukraine ..	226	165	12	-	150	327	9 Res. : 7 Sus.	0.50-0.30
Grand Total			1133 ²		922	2055	9 Res. : 7 Sus.	0.50-0.30
Bond \times Victoria ..	259	12	-	16	63	91	5 Res. : 11 Sus. ¹	1.00-0.90
Landhafer \times Bond	286	137	13	-	54	204	45 Res. : 19 Sus.	0.50-0.30

¹ Tests conducted at high temperatures modifying expected 9 res. : 7 sus. ratio.

² χ^2_4 heterogeneity for totals of 5 separate crosses = 1.96; P value = 0.80-0.70.

On this calculated basis the number of resistant and susceptible seedlings were 106.1 and 98.9 respectively (P value = 0.20-0.10); in the cross Burke \times Bond the corresponding numbers were 184.5 and 114.5 respectively (P value = 0.10-0.05). F_2 segregation in the cross Bond \times Victoria was studied at high temperatures with daily maxima in excess of 80°F. Under these environmental conditions the doubly heterozygous plants exhibited a "3" reaction type resulting in a 5 resistant : 11 susceptible F_2 ratio with which the observed segregation agreed statistically.

In the cross Landhafer \times Bond a ratio very close to 3 resistant : 1 susceptible was obtained. It was found, however, from F_3 studies to be reported later, that an alternative complementary factor from Landhafer interacted with one of the two Bond complementary genes. On this assumption the following genotypes were expected when segregation was studied in tests involving race 286 :

F_3 (Homozygous resistant)		F_2 (Resistant)	(Segregating)	(Susceptible)	(Homozygous susceptible)
1	Bd _a Bd _a Bd _b Bd _b Bd ₁ Bd ₁	2	Bd _a Bd _a Bd _b bd _b bd ₁ bd ₁	1	Bd _a Bd _a bd _b bd _b bd ₁ bd ₁
2	" " " " " bd ₁	4	" " " " " Bd ₁ bd ₁	2	" bd _a " " " " "
1	" " " " " bd ₁ bd ₁	2	" " " bd _b bd _b " "	1	bd _a " " " " "
2	" " Bd _b bd _b Bd ₁ Bd ₁	2	Bd _a bd _a Bd _b Bd _b Bd ₁ Bd ₁	1	" " Bd _b Bd _b Bd ₁ Bd ₁
1	" " bd _b " " "	4	" " " " " bd ₁	2	" " " " " bd ₁
		2	" " " " " bd ₁ bd ₁	1	" " " " " bd ₁ bd ₁
		4	" " Bd _b bd _b Bd ₁ Bd ₁	2	" " Bd _b bd _b Bd ₁ Bd ₁
		8	" " " " " bd ₁	4	" " " " " bd ₁
		4	" " " " " bd ₁ bd ₁	2	" " " " " bd ₁ bd ₁
		2	" " " bd _b bd _b Bd ₁ Bd ₁	1	" " " bd _b bd _b Bd ₁ Bd ₁
		4	" " " " " bd ₁	2	" " " " " bd ₁

In the F_2 therefore, a ratio of 45 resistant : 19 susceptible seedlings was expected and a satisfactory fit to this hypothesis was observed.

Relationship of F_2 seedling reaction types to different races was studied in the crosses Fulghum \times Bond and Burke \times Bond where inoculations on the primary leaves were carried out with mixtures of races 226, 259 and 286 and 226, 237 and 237-4 respectively. In no case was any marked variation in reaction type noted in the case of any F_2 seedling, indicating the operation of the same factors in Bond against all races in the mixtures.

(ii) Adult plant tests.

The F_2 segregation data for adult plant behaviour pertaining to the crosses of Bond with Fulghum, Algerian and Laggan are presented in Table 3.

TABLE 3

F₂ segregation for adult plant crown rust reaction in crosses involving Bond and certain susceptible varieties

Cross	Adult plant reactions			Total	Expected ratio	P value
	I ¹	R-MR	MS-S			
Fulghum \times Bond	65	29	35	129	3 Res. : 1 Sus.	0.70-0.50
Algerian \times Bond	82	39	54	175	3 Res. : 1 Sus.	0.10-0.05
Total	215	89	304	304	3 Res. : 1 Sus.	0.10-0.05
Laggan \times Bond	126	45	130	301	9 Res. : 7 Sus.	0.90-0.80

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

These figures confirmed the segregation of the two dominant complementary Bond factors in the cross Laggan \times Bond. However, the data for the other two crosses approximated a 3 resistant : 1 susceptible ratio indicating the action of a non-identical allele to one of the Bond genes in the varieties Algerian and Fulghum, operative in the adult plant stage only. The presence of such a factor in the variety Fulghum was confirmed from studies on the relationship of F_2

TABLE 4

Adult plant reactions of F₂ seedlings classified for reaction type to race 286 in crosses of Bond with Fulghum and Burke

Adult plant reaction	Seedling reaction types									
	Resistant			Susceptible 3-4	Resistant			Susceptible 3-4		
	0 ;	; - 1	1-2-		0 ;	; - 1	1-2-			
Fulghum × Bond									Burke × Bond	
I ¹	4	3	—	8	27	—	—	—
R	2	—	1	1	9	15	39	—
MR	2	1	2	1	4	—	4	2
Total ..			15	(17.0) ²		10 (9.0)	98 (100.0)			2 (0.0)
									Burke × Bond	
MS-S	1	1	—	11 (12.0)	—	—	2	27 (29.0)
			2 (0.0)				2 (0.0)			

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

² Expected values in brackets.

seedling reaction types and adult plant reactions, data for which are presented in Table 4 relating to crosses of Bond with Fulghum and Burke. In the cross Fulghum \times Bond with the operation of such a factor three out of seven susceptible seedlings would be expected to show resistance at the adult plant stage and all the resistant seedlings would be expected to maintain their resistance as mature

plants. From the resistant class of seedlings two were found to give a moderately susceptible mature plant reaction and these on progeny tests showed segregation. Obviously these were incorrectly classified. From among the susceptible seedlings, 10 compared with the nine expected out of 21 gave a resistant reaction due to the operation of the allele from Fulghum. In the cross Burke \times Bond two resistant seedlings out of 100 exhibited a moderately susceptible adult plant reaction and in this case also these were almost certainly due to incorrect classification. Similarly two susceptible seedlings produced moderately resistant adult plants, probably for similar reasons. Otherwise there was close agreement between seedling reaction types and adult plant reactions in this cross. It was thus concluded that the varieties Algerian and Fulghum possessed an effective allele to one of the complementary dominant factors in Bond and that Burke and Laggan carried the recessive allele at this locus.

(2) F_3 Seedling Segregation

Progeny tests were carried out on F_2 plants which had been classified for reaction type or randomly selected. Data for the different crosses are presented in Table 5. The expected reaction in all crosses except Landhafer \times Bond

TABLE 5

F_3 seedling behaviour for crown rust reaction in crosses involving Bond and certain susceptible varieties

Cross	Crown rust races	F_3 behaviour			Total	Expected ratio	P value
		Res. ¹	Seg.	Sus.			
Fulghum \times Bond	226 259 & 286						
(a) ²		3	22	13	38	1 Res.: 8 Seg.: 7 Sus.	0.50-0.30
(b)		11	65	64	140	1 Res.: 8 Seg.: 7 Sus.	0.70-0.50
	Total	14	87	77	178	1 Res.: 8 Seg.: 7 Sus.	0.70-0.50
Burke \times Bond	226 237-4 & 237						
(a)		8	57	35	100	1 Res.: 8 Seg.: 7 Sus.	0.30-0.20
(b)		8	70	49	127	1 Res.: 8 Seg.: 7 Sus.	0.50-0.30
	Total	16	127	84	227	1 Res.: 8 Seg.: 7 Sus.	0.20-0.10
Laggan \times Bond	226	10	119	109	237	1 Res.: 8 Seg.: 7 Sus.	0.50-0.30
Santa Fe \times Bond	286						
(b)		6	71 ³	72	149	1 Res.: 8 Seg.: 7 Sus.	0.50-0.30
(c)		12	79 ³	72	163	1 Res.: 8 Seg.: 7 Sus.	0.90-0.80
	Total	18	150	144	312	1 Res.: 8 Seg.: 7 Sus.	0.70-0.50
Bond \times Ukraine	286						
(b)		7	63 ³	68	138	1 Res.: 8 Seg.: 7 Sus.	0.50-0.30
Bond \times Victoria	259						
(b)		8	45 ³	56	109	1 Res.: 8 Seg.: 7 Sus.	0.20-0.10
	Grand Total	73	591	537	1201	1 Res.: 8 Seg.: 7 Sus.	0.80-0.70
Landhafer \times Bond	286						
(c)		12	70 ³	30	112	7 Res.: 38 Seg.: 19 Sus.	0.80-0.70

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² (a)=unclassified for F_2 phenotype, (b)=classified for F_2 seedling reaction type, (c)=classified for F_2 adult plant reaction.

³ Some lines in the segregating category showed a preponderance of susceptible plants.

was 1 homozygous resistant: 8 segregating: 7 homozygous susceptible lines. In the Landhafer \times Bond cross the corresponding expected ratio as shown previously was 7: 38: 19 respectively. In all cases there was satisfactory agreement statistically between observed and expected results. The confirmation of the predicted ratio in the Landhafer \times Bond cross indicated that Landhafer possessed a dominant factor complementary to one of the two dominant complementary genes in Bond.

In the crosses of Bond with Landhafer, Santa Fe, Ukraine and Victoria certain segregating F_3 lines showed a preponderance of susceptible seedlings. This was probably associated with high temperatures and was observed especially in tests conducted under glasshouse temperature regimes between 75°–85°F.

F_3 segregation was also studied in the progenies of F_2 plants classified for seedling reaction type to race 286 in crosses of Bond with Fulghum and Burke respectively, and these results are presented in Table 6. Good agreement was

TABLE 6

F₃ seedling behaviour for crown rust reaction of F₂ plants classified for seedling reaction type in crosses involving Bond with Fulghum and Burke

F_2 reaction types to race 286						F_3 behaviour to mixture of races					
						226, 259 and 286			226, 237 and 237-4		
						Res. ¹	Seg.	Sus.	Res.	Seg.	Sus.
						Fulghum × Bond			Burke × Bond		
0;	12	28	1	10	29	—
;- 1	—	34	—	1	14	—
1-2-	—	4	—	—	39	1
3-4	—	2	59	—	4	29

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

shown between F_2 reaction type and expected F_3 segregation except for two instances, one in each cross, where a resistant F_2 plant gave homozygous susceptible progenies. These were probably errors in F_2 classification. Similarly a few plants classified as susceptible in F_2 gave segregating F_3 progenies. This may have been due to high temperature effects resulting in heterozygous genotypes involving Bond genes being classified as susceptible.

(c) *Behaviour of Segregating Generations Involving Races to which both Bond and the Second Parent were Resistant*

(1) F_2 Segregation

(i) Seedling tests.

The varieties Landhafer, Santa Fe and Ukraine each possessed a single factor for seedling resistance to races to which they were resistant. The F_2 segregation in the cross Landhafer × Bond in tests involving race 286 to which Landhafer was susceptible conformed to 45 resistant : 19 susceptible. Therefore with the operation of one additional dominant factor in Landhafer in tests involving races to which it also was resistant the expected F_2 ratio was 237 resistant : 19 susceptible; if allelism was involved the expected ratio would be modified to a characteristic dihybrid ratio of 15 resistant : 1 susceptible. In the case of crosses between Bond and both Santa Fe and Ukraine the ratio conformed statistically to a 15 : 1 rather than 57 : 7 ratio. Hence against races to which either Santa Fe or Ukraine were respectively resistant a non-identical allele to one of the two complementary factors in Bond was operative. These were alleles rather than identical genes since the factor in Ukraine conferred resistance to fewer races.

The F_2 segregation of the Victoria type of rust resistance in crosses with susceptible varieties was 71.9 resistant : 28.1 susceptible; with the operation of the two complementary Bond factors only 12.3 per cent of plants were expected to be susceptible. Since partial dominance was exhibited by the majority of factors in both Bond and Victoria, the intermediate and resistant classes were grouped together for goodness of fit tests.

TABLE 7
F₂ seedling segregation for crown rust reaction in crosses involving Bond and certain varieties utilising races to which both parents were resistant

Cross	Crown rust race	F ₂ reaction types				Expected ratio	P value
		0 ; - ;	Resistant ; - 1 -	2 -	Susceptible 3 - 4	Total	
Landhafer × Bond	..	406	19	—	25	237 Res. ¹ ; 19 Sus.	0.20-0.10
	226	80	17	—	11	237 Res.; 19 Sus.	0.30-0.20
	237-4	153	27	1	15	237 Res.; 19 Sus.	0.90-0.80
	259	174	17	—	14	237 Res.; 19 Sus.	0.80-0.70
Total		813	80	1	65	237 Res.; 19 Sus.	0.50-0.30
Santa Fe × Bond	105	48	13	7	57 Res.; 7 Sus.	0.30-0.20
	226	212	47	—	11	57 Res.; 7 Sus.	0.20-0.10
	237-4	299	200	51	32	57 Res.; 7 Sus.	0.50-0.30
	259	616	295	64	50	57 Res.; 7 Sus.	0.10-0.05
Total		192	975	7	20	57 Res.; 7 Sus.	1.00-0.90
Bond × Ukriane	56	25	11	23	71.9 Res.; 28.1 Sus.	0.02-0.01
	226	80	55	6	23	71.9 Res.; 28.1 Sus.	0.70-0.50
	237-4	99	61	32	26	71.9 Res.; 28.1 Sus.	0.90-0.80
	286	235	141	49	72	71.9 Res.; 28.1 Sus.	0.20-0.10
Total		425	425				

¹ Res. = resistant, Sus. = susceptible.

The data for F_2 seedling segregation in crosses of Bond with Landhafer, Santa Fe, Ukraine and Victoria are presented in Table 7. Statistical tests showed good agreement between observed and expected results except in tests employing race 226 in the cross Bond \times Victoria.

(ii) Adult plant tests.

F_2 generations of crosses involving Bond with Landhafer, Santa Fe and Victoria respectively were classified for mature plant field reactions and the data are presented in Table 8. With the operation of an additional partially dominant factor in Landhafer the expected F_2 ratio in this cross was 1005 resistant: 19 susceptible. In the cross Santa Fe \times Bond a corresponding 15

TABLE 8

F_2 segregation for adult plant crown rust reaction in crosses involving Bond and certain varieties utilising races to which both parents were resistant

Cross	Adult plant reactions					Total	Expected ratio	P value
	Resistant			Susceptible				
	I ¹	R	MR	MS	S			
Landhafer × Bond	231	28	—	3	5	267	1005 Res. ² : 19 Sus.	0.20-0.10
Santa Fe × Bond	483	122	18	7	26	656	15 Res. : 1 Sus.	0.20-0.10
Bond × Victoria ..	273	15	—	2	3	293	97.4 Res. : 2.6 Sus.	0.50-0.30

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

² Res.=resistant, Sus.=susceptible.

resistant: 1 susceptible ratio was expected; in the cross Bond \times Victoria the expected percentage of susceptible plants was 2.6 (or seven-sixteenths of 5.92%).

Statistical agreement between observed and expected results was good as shown in Table 8. However it was subsequently observed in progeny tests

TABLE 9

F_3 seedling behaviour for crown rust reaction in crosses involving Bond and certain varieties utilising races to which both parents were resistant

Cross	Crown rust race	Res. ¹ Seg. Sus.				Total	Expected ratio	P value
		Res.	Seg.	Sus.				
Landhafer \times Bond								
(a) ²	259	39	62	6	107	65	Res.: 152 Seg.: 19 Sus.	0.70-0.50
(b)	259	10	15	2	27	65	Res.: 152 Seg.: 19 Sus.	1.00-0.90
	Total	49	77	8	134	65	Res.: 152 Seg.: 19 Sus.	0.70-0.50
Santa Fe \times Bond								
(a)	259	49	62	6	117	7	Res.: 8 Seg.: 1 Sus.	0.80-0.70
(b)		64	74	9	147	7	Res.: 8 Seg.: 1 Sus.	1.00-0.90
	Total	113	136	15	264	7	Res.: 8 Seg.: 1 Sus.	0.90-0.80
Bond \times Ukraine								
(b)	237 & 237-4	51	49	9	109	7	Res.: 8 Seg.: 1 Sus.	0.50-0.30
Bond \times Victoria								
(a)	226 &	13	32	6	51	25.5	Res.: 62.2 Seg.: 12.3 Sus.	1.00-0.90
(b)	286	27	59	16	102	25.5	Res.: 62.2 Seg.: 12.3 Sus.	0.70-0.50
	Total	40	91	22	153	25.5	Res.: 62.2 Seg.: 12.3 Sus.	0.70-0.50

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² (a)= F_2 material classified for adult plant reaction; (b)= F_2 material classified for seedling reaction type.

of the susceptible plants from the cross Landhafer \times Bond that one segregated for the Bond type of resistance and susceptibility, one for the Landhafer type of resistance and susceptibility, whilst one was homozygous resistant for the Landhafer reaction type. This was probably due to the fact that the gene allelic to the dominant complementary factor in Bond was not operative at the adult plant stage. On this hypothesis the expected F_2 ratio was 249 resistant : 7 susceptible; on the sample tested this ratio could not be statistically distinguished from the respective 1005 : 19 ratio previously hypothesized.

Correlated behaviour of F_2 seedlings and adult plants in the cross Bond \times Ukraine is presented later.

(2) F_3 Segregation

Representative samples of plants from each reaction class were tested for random F_2 progeny behaviour in various crosses. The observed and calculated expected frequencies of F_3 lines are presented in Table 9. The expected ratios in the different crosses were as follows :

	Homozygous resistant	Segregating	Homozygous susceptible
Landhafer \times Bond	85	152	19
Santa Fe or Ukraine \times Bond	7	8	1
Victoria \times Bond	25.5	62.2	12.3

Results showed good agreement between observed and expected results and confirmed assumptions that in the different crosses various factors conditioning seedling resistance were operative as follows :

In the cross Bond \times Landhafer, Bond contributed two dominant complementary factors; the variety Landhafer contributed two factors one of which acted in a dominant complementary manner to one of the two factors in Bond, the second being independent and dominant. The varieties Santa Fe and Ukraine also had one independent dominant factor but possessed a complementary allele to one of the two Bond factors. The genes were allelic and not identical for reasons previously indicated. In the cross Bond \times Victoria there were no interactions between the factors contributed by the two varieties and in all six factors were concerned in conditioning seedling resistant in this cross.

(d) *Relationship of F_2 or F_3 Segregating Reactions and Reaction Types to Different Races, Between Segregating Seedling and Adult Plants, and Between F_2 and F_3 Segregating Generations*

(1) F_2 Seedling compared with F_2 Seedling

Inoculations were made on the primary leaf with a rust race to which both parents were resistant, and the secondary leaves inoculated with a race to which only Bond was resistant. The results from such studies involving three crosses are set out in Table 10. In all instances the susceptible classes were susceptible to both races. The majority of seedlings exhibiting an intermediate reaction type on the primary leaf showed full susceptibility on the secondary leaves, indicating that they possessed factors for resistance from the parent other than Bond. Some seedlings from this category, however, showed the Bond reaction type to races to which only Bond was resistant, indicating only partial dominance of the Bond genotype or the action of modifying genes. Considering the total resistant class the expected fractions of F_2 plants susceptible to the second race were thus :

Cross	Landhafer \times Bond	—57/237
Cross	Santa Fe \times Bond	—24/60
Cross	Bond \times Ukraine	—24/60

In all three crosses the deviations were not statistically significant at the 5% probability level.

TABLE 10
Association of F₂ seedling reaction types in Bond crosses between tests involving races to which both parents were resistant and those involving races to which only Bond was resistant

F ₂ reaction types (both parents resistant)	F ₂ reaction types (only Bond resistant)					
	Race 286		Race 286		Race 286	
	Resistant 0 ; —	Susceptible — 1 3-4	Resistant 0 ; —	Susceptible — 1 3-4	Resistant 0 ; —	Susceptible — 1 3-4
0 ; - ; - 1	Landhafer × Bond		Santa Fe × Bond		Bond × Ukraine	
	133 4	13 28 13	146 2	— 3 65 42	24 —	23 7
3-4	Total		Total		Total	
	150 —	41 (45·9) ² 13	151 —	107 (103·2) ³ 11	27 —	30 (22·8) ⁴ 1

¹ Expected values in brackets.
² P value=0·50-0·30 ; ³ P value=0·70-0·50 ; ⁴ P value=0·10-0·05.

One interesting observation was noted in the cross Bond \times Ukraine when F_2 seedlings classified for reaction type to races 237-4 and 226 were reinoculated with race 286 fifty-two days after sowing. All resistant seedlings maintained their resistance whereas of the seedlings susceptible to race 226, 16 out of 28 were resistant to race 286. This shows perfect agreement with the 15.7 resistant plants expected on the assumption that the complementary factors for adult plant resistance in Ukraine were operative at this stage of growth. Presumably the third factor conditioning adult plant resistance in Ukraine was not operative against this race.

(2) F_2 Seedling compared with F_2 Adult Plant

Seedlings classified for reaction type in crosses of Bond with Santa Fe, Ukraine and Victoria were transplanted for observations on adult plant field reactions, and the data are presented in Table 11.

The assumptions relating to gene behaviour in different crosses were:

In the cross Santa Fe \times Bond the factors operative in the seedling stage conditioned adult plant resistance in addition; the complementary allele in Santa Fe, operative in the adult stage only, resulted in all resistant seedlings maintaining their resistance and the susceptible seedling group proving susceptible subsequently.

In the cross Bond \times Ukraine, the seedling resistance Ukraine factor operated against few races only and was ineffective in conditioning adult plant resistance in the field where several races were involved. The three factors in this variety conditioning only adult plant resistance were operative. The complementary allele was also effective in Ukraine (the comparable factors in Fulghum and in Santa Fe behaving similarly), the resistant seedling class producing 21 susceptible adult plants in a population of 960 and the susceptible seedling category 57 resistant plants in a population of 64.

In the cross Bond \times Victoria 56.25 per cent of seedlings maintained their resistance due to the operation of the Bond factors. On the 31.45 per cent resistant due to segregation of factors from Victoria, 0.55 were susceptible and of the 12.3 per cent susceptible seedlings 2.04 were susceptible as mature plants.

From the data presented in Table 11 two plants in each of the crosses Santa Fe \times Bond and Bond \times Ukraine did not behave exactly as expected. The reaction type class “;”-“1” in the cross Bond \times Ukraine was considered to possess the Ukraine type of resistance on the basis of F_3 progeny reaction types. No statistically significant deviations were obtained. No susceptible adult plants were observed in the Victoria type seedling reaction group; however, since in the population examined only 0.8 was expected, this deviation was clearly not significant.

(3) F_2 Seedling compared with F_3 Seedling

Certain F_2 plants were classified for reaction type to races to which both parents were resistant and their F_3 progenies tested against similar races or against a specific race to which Bond alone was resistant. The information obtained in this regard is set out in Table 12 and shows that two plants, one each in the crosses Bond \times Ukraine and Bond \times Victoria, from the resistant F_2 category yielded susceptible progenies in tests involving races to which both parents were resistant. One line in the cross Bond \times Victoria from the susceptible F_2 class segregated with a preponderance of susceptible plants indicating the operation of the factor Vc_2 and its linked inhibitor.

In tests involving races to which Bond alone was resistant the only lack of correlation was that shown when a homozygous resistant line with a reaction type similar to Bond was derived from an F_2 plant exhibiting an intermediate reaction type. Apart from this discrepancy the behaviour of plants of an

TABLE 11
Adult plant reactions of F_2 seedlings classified for reaction type in crosses involving Bond with Santa Fe, Ukraine and Victoria

Adult plant reactions	Seedling reaction types							
	Santa Fe \times Bond		Bond \times Ukraine		Bond \times Victoria			
	0 ;	72 (73.0) ²	3-4	0 ;	72 (74.0)	0 ; -1	3-4	3-4
I ¹ , R, MR	..	61 (61.0)	1 (0.0)	72 (74.0)	70 (68.8)	57 (57.0)	13 (16.0)	10 (10.0)
MS-S	..	1 (0.0)	9 (10.0)	2 (0.0)	2 (3.2) ³	—	5 (2.0) ⁴	2 (2.0) ⁶

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

² Expected values in brackets.

³ P value=0.70-0.50

⁴ P value=0.10-0.05

⁵ P value=0.80-0.70 } χ^2 values corrected for small numbers.

⁶ P value=1.00.

intermediate reaction type was as expected, progenies segregating for Bond genes or homozygous susceptible lines being produced, indicating the presence of factors contributed by the second parent.

(4) F_2 Adult Plant compared with F_3 Seedling

The F_2 segregation pattern in the cross Landhafer \times Bond was based on the operation of five factors, two from Bond and three from Landhafer. Of

TABLE 12

F_3 seedling behaviour for crown rust reaction of F_2 plants classified for seedling reaction type in crosses involving Bond when tested against various races

	F_2 reaction types to races to which both parents were resistant	F_3 behaviour to					
		races to which both parents were resistant			races to which only Bond was resistant		
		Res. ¹	Seg.	Sus.	Res.	Seg.	Sus.
Landhafer \times Bond	Race 226						
	0 ;	6	10	—	1	17	5
	; - 1	2	1	—	1	1	1
	3 - 4	—	—	8	—	—	8
Santa Fe \times Bond	Race 259						
	0 ;	26	40	—	5	58	3
	; - 1	33	14	—	—	3	46
	2 -	1	23	—	—	—	25
	3 - 4	—	—	9	—	—	9
Bond \times Ukraine	Race 237-4						
	0 ;	32	27	1	7	61	6
	; - 1	17	19	—	—	1	47
	3 - 4	—	—	12	—	—	16
Bond \times Victoria	Race 237-4						
	0 ;	21	36	—	9	48	2
	; - 1	7	8	1	—	3	18
	2 -	2	16	—	—	—	18
	3 - 4	—	1 ²	10	—	—	11

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² Segregating with preponderance of susceptible seedlings.

these one factor in Landhafer conditioned adult plant resistance only. While the susceptible F_2 plants were therefore expected to produce only susceptible F_3 seedling progenies in tests involving races to which both parents were resistant, some resistant F_2 adult plants when similarly tested were expected to yield susceptible seedling progenies. From data presented in Table 13, containing information pertinent to this correlated study, some F_2 susceptible plants gave either homozygous resistant or segregating lines due to segregation of the Bond factors effective against race 286. These were presumed errors in F_2 classification or labelling. Statistically good agreement between observed and expected results in the segregation of resistant F_2 plants was obtained on the basis of expected ratios of 112 homozygous resistant : 608 segregating : 285 homozygous susceptible and 340 homozygous resistant : 608 segregating : 57 homozygous susceptible lines in tests involving races 286 and 259 respectively.

In the cross Santa Fe \times Bond two factors in Bond and two in Santa Fe, one allelic to one of the Bond factors, were effective in conditioning both seedling and adult plant resistance. Hence susceptible F_2 adult plants would be expected to produce homozygous susceptible F_3 lines and resistant plants to yield homozygous resistant progenies or segregating lines in tests involving races to which both parents were resistant. Probably due to misclassification two in the population of 103 resistant plants produced susceptible progenies and of

the 14 susceptible plants three gave segregating progenies. The former two plants were moderately resistant and the latter three moderately susceptible and all were probably minor misclassifications. It was evident, however, that the same factors conditioned both seedling and adult plant resistance in Bond and also Santa Fe.

TABLE 13

F₃ seedling behaviour for crown rust reaction of F₂ plants from the cross Landhafer × Bond classified for adult plant reaction

Adult plant reactions			F ₃ behaviour to					
			races to which only Bond was resistant			races to which both Bond and Landhafer were resistant		
			Race 286			Race 259		
			Res. ¹	Seg.	Sus.	Res.	Seg.	Sus.
I ²	11	62	15	33	48	2
R-MR	—	2	16	2	13	3
Total			11	64	31	35	61	5
Expected			11.8	64.1	30.1	34.2	61.1	5.7
MS-S	—	1	6	1	1	4

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

In the cross Bond × Victoria, due to the operation of the factors from Victoria conferring mature plant resistance, only one quarter of the total population, in which the proportion of resistant plants was seven-sixteenths, was expected to give susceptible F₃ seedling progenies in tests involving races to which both parents were resistant and similarly one-fifth of the susceptible F₂ class was expected to produce segregating F₃ lines. Of the 209 plants tested from the former class, 21 gave susceptible progenies compared with 21.4 expected. Since only five susceptible F₂ plants were progeny tested, the fact that no segregating line was observed was obviously not a significant discrepancy since only one was expected.

(5) F₃ Seedling compared with F₃ Seedling

In the four crosses involving Bond parentage approximately 25 seeds of each F₃ line were tested to one race to which both parents were resistant and a similar sample tested to a second race to which only Bond was resistant. The various frequencies and interrelationships on the genetic bases previously formulated were as follows:

Cross	Behaviour to races to which both parents were resistant				Behaviour to race to which only Bond was resistant			
					Homo. Res.	Seg.	Homo. Res.	Total
Landhafer × Bond	..	Homo. Res.	28	38	19	85
		Seg.	—	114	38	152
		Homo. Sus.	—	—	19	19
		Total	28	152	76	256
Santa Fe × Bond and Bond × Ukraine	..	Homo. Res.	4	14	10	28
	..	Seg.	—	18	14	32
		Homo. Sus.	—	—	4	4
		Total	4	32	28	64
Bond × Victoria	..	Homo. Res.	6.25	10.25	9.0	25.5
		Seg.	—	39.75	22.5	62.25
		Homo. Sus.	—	—	12.25	12.25
		Total	6.25	50.0	43.75	100.0

The observed and expected frequencies, in brackets, are shown in Table 14. Since the F_2 population was classified for reaction type to a race to which both parents were resistant, the expected frequencies were calculated separately within the total of each reaction type class to races to which both parents were resistant and not for the overall totals. There was good agreement between observed and expected results in all crosses except Santa Fe \times Bond. In every test homozygous susceptible lines to one race invariably behaved similarly to the second race. One line in each of the crosses Bond \times Ukraine and Bond \times Victoria segregated to the race to which both parents were resistant but was homozygous resistant to the second race. This may have been due to insufficient plants being tested to detect susceptible seedlings in a line actually segregating; in this case the line would be designated erroneously as homozygous resistant.

TABLE 14

Correlation of F_3 seedling crown rust behaviour in Bond crosses between tests involving races to which both parents were resistant and those involving races to which only Bond was resistant

Cross	F_3 reactions to race to which both parents were resistant	F_3 reactions to race to which only Bond was resistant			Total	P value
		Res. ¹	Seg.	Sus.		
Landhafer \times Bond	Race 259		Race 286			
	Res.	12 (15.1) ²	24 (20.6)	10 (10.3)	46	0.50-0.30
	Seg.	—	52 (57.8)	25 (19.2)	77	0.20-0.10
	Sus.	—	—	13	13	
Santa Fe \times Bond	Res.	11 (13.9)	26 (48.9)	60 (34.6)	97	<0.001
	Seg.	—	86 (75.9)	49 (59.1)	135	0.10-0.05
	Sus.	—	—	21	21	
Bond \times Ukraine	Race 237 and 237-4		Race 286			
	Res.	6 (7.1)	25 (25.0)	19 (17.9)	50	0.90-0.80
	Seg.	1 (0.0)	25 (25.3)	19 (19.7)	45	0.90-0.80
	Sus.	—	—	16	16	
Bond \times Victoria	Race 226		Race 259			
	Res.	5 (7.4)	17 (12.0)	8 (10.4)	30	0.20-0.10
	Seg.	1 (0.0)	35 (40.2)	28 (22.8)	64	0.30-0.20
	Sus.	—	—	11	11	

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² Expected values in brackets.

In the cross Santa Fe \times Bond there was a statistically highly significant deviation from the expected results due mainly to an excess in the number of lines homozygous resistant to race 259 and homozygous susceptible to race 286 over that calculated. This is difficult to explain since the number of lines homozygous resistant to both races was close to that expected. The F_3 ratios in tests involving the two races independently from data presented in Tables 5 and 9 also showed good agreement on the basis of the hypotheses proposed.

(B) *Association between crown rust resistance factors in Bond and stem rust resistance factors in Burke and Laggan*

In the crosses Burke \times Bond and Laggan \times Bond 228 and 235 F_3 lines respectively were tested against race 259 of crown rust and a mixture of races 2 and 12 of oat stem rust. The independent behaviour of genes governing crown rust resistance in Bond and the gene (Rd₁) conditioning stem rust resistance in both Burke and Laggan is clear from the data presented in Table 15.

(C) *Inheritance of grass clump habit and its association with the inheritance of crown rust resistance in the cross Landhafer × Bond*

In F_2 adult plants in the cross Landhafer × Bond 49 in a total of 267 plants showed a grass clump habit of growth. These numbers agreed statistically with a ratio of 13 normal : 3 grass clump ($P=0.90-0.80$) suggesting the action of an inhibitor gene to a dominant gene for grass clumping. Similar gene

TABLE 15

Association of F_3 stem rust and crown rust reactions in crosses of Bond with Burke and Laggan

Stem rust behaviour	Crown rust behaviour							
	Burke × Bond			Total	Laggan × Bond			Total
	Res. ¹	Seg.	Sus.		Res.	Seg.	Sus.	
Res. ..	6 (5.4) ²	36 (38.2)	19 (17.4)	61	1 (1.9)	27 (25.6)	23 (23.5)	51
Seg. ..	10 (10.4)	70 (70.4)	38 (33.2)	118	4 (4.8)	61 (63.3)	61 (57.9)	126
Sus. ..	4 (4.2)	37 (30.4)	8 (14.4)	49	4 (2.3)	30 (29.1)	24 (26.6)	58
Total	20	143	65	228 ³	9	118	108	235 ⁴

¹ Res.=homozygous resistant, Seg.=segregating, Sus.=homozygous susceptible.

² Expected values in brackets based on marginal totals.

³ $\chi^2_4 = 3.56$; $P=0.50-0.30$.

⁴ $\chi^2_4 = 2.43$; $P=0.70-0.50$.

action for grass clump habit has been observed in wheat crosses (McMillan, 1937; Watson, 1943). The independence of genes determining this character from those conditioning adult plant resistance in Bond and Landhafer is shown from the data in Table 16. A number of weak F_2 plants were observed and

TABLE 16

Association of adult plant reaction to crown rust and grass clump habit in the F_2 generation of a cross between Bond and Landhafer

Adult plant reactions				Growth habit		Grass clump	Total
				Normal	Weak		
I ¹		147 (147.1) ²	40 (41.5)	44 (42.4)	231
R-MR		17 (17.8)	7 (5.0)	4 (5.2)	28
MS-S		6 (5.1)	1 (1.5)	1 (1.4)	8
		Total		218	49		267 ³
		Expected ratio		216.9		50.1 ⁴	
		(13 normal : 3 grass clump)					

¹ I=immune, R=resistant, MR=moderately resistant, MS=moderately susceptible, S=susceptible.

² Expected values in brackets based on marginal totals.

³ χ^2_4 for independence=1.67; $P=0.90-0.80$.

⁴ $\chi^2_4 = 0.03$; $P=0.90-0.80$.

these may have been heterozygous for the inhibitor gene in the presence of the dominant factor for grass clumping, indicating partial epistasis.

DISCUSSION AND CONCLUSIONS

From the present studies it is evident that the immunity of Bond to Australian races of crown rust in both seedling and adult plant stages was conditioned by two dominant complementary genes. However, dominance was incomplete at high temperatures and the genotype heterozygous for both factors

gave a moderately susceptible reaction type modifying the characteristic 9 resistant: 7 susceptible F_2 ratio to a respective 5: 11 ratio. These findings are in accordance with the observations of other investigators, including Hayes *et al.* (1939) and Weetman (1942). It is proposed to designate these factors as \underline{Bd}_a and \underline{Bd}_b , the line below each symbol indicating complementary gene action. Presumably one gene was contributed by each of the parents, Golden Rain and Red Algerian selection, to the hybrid from which it was selected. Segregation in a cross between Bond and Golden Rain is currently being studied to investigate this hypothesis.

Operation of a single factor was observed in a number of intervarietal crosses involving Bond. In its crosses with Algerian and Fulghum at the mature plant stage monogenic segregation was observed, whilst in crosses with Santa Fe and Ukraine, involving races to which these varieties were also resistant, duplicate factor segregation was noted. Hayes *et al.* (1939) assumed the presence of a common factor in such crosses, Finkner *et al.* (1955) only a single factor in both varieties whilst Osler and Hayes (1953) and Weetman (1942) detected the presence of factors in Santa Fe and Ukraine allelic to one of the Bond genes. The present studies confirmed the latter findings since the complementary factors in Bond were operative in the seedling stage against races to which the second parent was susceptible. It was also evident that the alleles in the varieties Algerian, Fulghum, Santa Fe and Ukraine were not identical since they were operative only against the races to which the respective parents were resistant, either in both seedling and adult plant stages or in the mature plant stage only.

These studies extended the genes for crown rust resistance identified in certain varieties. The complete genotypes of these varieties for crown rust resistance are given below, where non-interacting genes are indicated by numerical suffixes, interacting (complementary) genes given alphabetical suffixes and allelomorphous genes indicated by apostrophe (') marks according to increasing order of reaction type or reaction. Torrie (1939) claimed that Bond possessed one strong gene and that another masked its effect. If Torrie's strong gene in Bond is that designated as \underline{Bd}_a the alleles in the present instance would be relative to the second Bond factor \underline{Bd}_b . Those in Santa Fe, Ukraine and Fulghum would in the proposed terminology be designated as \underline{Bd}_b' , \underline{Bd}_b'' and \underline{Bd}_b''' respectively. Similarly the alternative gene in Landhafer, assumed to act in complementary fashion with \underline{Bd}_a would be designated \underline{Bd}_L . This factor was also operative against race 236 to which Landhafer was susceptible. The complete list of genes, including those documented by Upadhyaya and Baker (1965), in varieties in which additional factors were revealed in Bond crosses are thus:

Landhafer—three factors. One factor (Ld_1) conditioned seedling as well as adult plant resistance. A second factor Ld_2 was responsible for adult plant resistance only and the third factor \underline{Bd}_L was an alternate complementary factor to one (\underline{Bd}_a) of the two complementary Bond factors in conditioning seedling resistance only.

Santa Fe—three factors. One factor (Sf_1) conditioned seedling as well as adult plant resistance. A second factor (\underline{Tr}_a) acting in complementary fashion with \underline{Tr}_b in *Trispermia* inhibited the action of Sf_1 against race 203 in the seedling stage only. The third factor \underline{Bd}_b' was complementary in action with \underline{Bd}_a and allelic to \underline{Bd}_b . This factor conditioned seedling resistance to races to which Santa Fe was resistant and also resistance in the adult plant stage.

Ukraine—five factors. One factor Sf_1' , allelic with Sf_1 , conditioned only seedling resistance to race 237. Three genes $\underline{M\bar{u}}_1$, $\underline{M\bar{u}}_a$ and $\underline{M\bar{u}}_b$, conferred

adult plant resistance only, the two latter factors acting in complementary fashion. The fifth factor Bd_b'' was a member of the allelic series at the Bd_b locus.

Fulghum and Algerian—one gene. The Bd_b''' member of the allelic series at this locus acted in complementary fashion with the gene Bd_a to confer adult plant resistance only.

The genes previously identified in *Trispermia* were Sf₁'', allelic with Sf₁, but exhibiting a higher reaction type, and Tr_b complementary to Tr_a.

No variety used in these studies or those previously reported in this series of papers was resistant to all Australian races of crown rust and the allelism indicated is obviously a barrier in attempts to combine genes from different varieties to provide a more comprehensive genetic basis for resistance in breeding commercial varieties.

The order of epistasis or dominance in the varieties studied in this series of papers was Bond (immune); Landhafer, Santa Fe, Ukraine (highly resistant); *Trispermia*, Victoria (resistant); Fulghum, Algerian, Burke, Laggan (susceptible).

Plants of a grass clump habit were observed in the F₂ generation of the cross Bond × Landhafer. Coffman (1964) detected dwarf segregates, some apparently of grass clump or grass tuft habit, in certain intervarietal crosses. He considered dwarfing in general to be due to one, two or three gene pairs with various types of interaction when more than one gene was implicated.

References

- BAKER, E. P., and UPADHYAYA, Y. M., 1955.—Physiologic specialisation of crown rust of oats. *Proc. Linn. Soc. N.S.W.*, 80: 340–357.
- COCHRAN, G. W., JOHNSON, C. O., HYENE, E. G., and HANSING, E. G., 1945.—Inheritance of reaction to smut, stem rust and crown rust in four oat crosses. *Jour. agric. Res.*, 70: 43–61.
- COFFMAN, F. A., 1964.—Inheritance of morphologic characters in *Avena*. United States Dept. Agric. tech. Bull. No. 1308.
- FINKNER, V. C., 1954.—Genetic factors governing resistance and susceptibility of oats to *Puccinia coronata* Corda variety *avenae*, F. & L., Race 57. Iowa State Coll. agric. Expt. Stat. Res. Bull., 411: 1040–1063.
- GRIFFITHS, D. J., 1953.—Varietal resistance and susceptibility of oats to crown rust. *Plant Pathology*, 2: 73–77.
- HAYES, H. K., MOORE, M. B., and STAKMAN, E. C., 1939.—Studies of inheritance in crosses between Bond, *A. byzantina* and varieties of *A. sativa*. Minn. agri. expt. stat. tech. Bull. 137.
- KEHR, W. R., and HAYES, H. K., 1950.—Studies of inheritance in crosses between Landhafer, *A. byzantina* L. and two selections of *A. sativa* L. *Agron. Jour.*, 42: 71–78.
- KO, S. Y., TORRIE, J. H., and DICKSON, J. C., 1946.—Inheritance of reaction to crown rust and stem rust and other characters in crosses between Bond, *A. byzantina*, and varieties of *A. sativa*. *Phytopath.*, 36: 226–235.
- LITZENBERGER, S. C., 1949.—Inheritance of resistance to specific races of crown rust and stem rust, to *Helminthosporium* blight and of certain other agronomic characters of oats. Iowa agri. Expt. Stat. Res. Bull. 370.
- McMILLAN, J. R. A., 1937.—Investigations on the occurrence and inheritance of the grass clump character in crosses between varieties of *T. vulgare* (Vill.). Coun. sci. industr. Res. Melbourne, Bull. 104.
- OSLER, R. C., and HAYES, H. K., 1953.—Inheritance studies in oats with particular reference to Santa Fe type of crown rust resistance. *Agron. Jour.*, 45: 49–53.
- TORRIE, J. H., 1939.—Correlated inheritance in oats of reaction to smuts, crown rust, stem rust and other characters. *Jour. agric. Res.*, 59: 783–804.
- UPADHYAYA, Y. M., and BAKER, E. P., 1960.—Studies on the mode of inheritance of Hajira type stem rust resistance and Victoria type crown rust resistance as exhibited in crosses involving the oat variety Garry. *Proc. Linn. Soc. N.S.W.*, 85: 157–179.
- , 1962a.—Studies on the inheritance of rust resistance in oats. I. Inheritance of stem rust resistance in crosses involving the varieties Burke, Laggan, White Tartar and Anthony. *Proc. Linn. Soc. N.S.W.*, 87: 141–147.
- , 1962b.—Studies on the inheritance of rust resistance in oats. II. The mode of inheritance of crown rust resistance in the varieties Landhafer, Santa Fe, Mutica Ukraine, *Trispermia* and Victoria in their crosses with susceptible varieties. *Proc. Linn. Soc. N.S.W.*, 87: 200–219.

- UPADHYAYA, Y. M., and BAKER, E. P., 1965.—Studies on the inheritance of rust resistance in oats. III. Genetic diversity in the varieties Landhafer, Santa Fe, Mutica Ukraine, Trispermia and Victoria for crown rust resistance. *PROC. LINN. Soc. N.S.W.*, 90 : 129–151.
- WATERHOUSE, W. L., 1938.—Some aspects of problems in breeding for rust resistance in cereals. *Jour. roy. Soc. N.S.W.*, 72 : 7–54.
- , 1952.—Australian Rust Studies. IX. Physiologic race determinations and surveys of cereal rusts. *PROC. LINN. Soc. N.S.W.*, 77 : 209–258.
- WATSON, I. A., 1943.—Inheritance studies with Kenya varieties of *Triticum vulgare* Vill. *Proc. LINN. Soc. N.S.W.*, 68 : 72–90.
- WEETMAN, I. M., 1942.—Genetic studies in oats of resistance to two physiologic races of crown rust. *Phytopath.*, 32 : 19 (abst.).